THE ARCHAEOTROGONIDAE OF THE EOCENE AND OLIGOCENE PHOSPHORITES DU QUERCY (FRANCE)[1]

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ABSTRACT: The genus *Archaeotrogon* Milne-Edwards was described in the last century from the fossiliferous deposits of "Phosphorites du Quercy." New excavations carried out at these sites have resulted in additional avian specimens that we have been able to assign to the three previously described species of *Archaeotrogon*. The temporal distribution of these species is discussed, and a new species is described.

The species of *Archaeotrogon* do not have the heterodactyl structure of the foot characteristic of modern trogons, although this structure had already been acquired in some contemporaneous forms. It appears that archaeotrogons constituted a distinct family, the Archaeotrogonidae, that evolved parallel with the family Trogonidae, or true trogons.

RESUME: Le genre *Archaeotrogon* Milne-Edwards a été décrit au siècle dernier dans les gisements des Phosphorites du Quercy. De nouvelles fouilles effectuées dans ces gisements ont permis de retrouver les trois espèces précédemment signalées et de leur attribuer un certain nombre d'éléments du squelette. Leur position chronologique a pu être précisée et une nouvelle espèce a été décrite.

Les *Archaeotrogon* ne présentent pas la structure du pied hétérodactyle caractéristique des trogons actuels bien que cette structure soit déjà acquise chez des formes fossiles du même âge. On peut donc penser que les *Archaeotrogon* constituent une famille différente ayant évolué parallèlement à celle des Trogonidae ou vrais trogons.

The "Phosphorites du Quercy" are deposits that filled sinkholes in the karst topography of the departments of Tarn-et-Garonne, Lot, and Aveyron, to the southwest of the central French massif. These deposits were very actively exploited for the extraction of calcium phosphate between approximately 1870 and 1880. During the course of mining, many specimens of fossil vertebrates, as well as molluscs and insects, were discovered in these localized deposits. The first discoveries of bird bones were announced by Lydekker (1891), followed by Milne-Edwards (1892). The birds of the Phosphorites du Quercy were thereafter the subject of an important work by Gaillard (1908). But the bones of the early collections did not bear precise data as to which sinkhole they were collected from, and the phosphorite deposits at Quercy include faunas that extend from the Upper Bartonian (Robiac's mammal zone) all the way to the Upper Stampian (Boningen's mammal zone).

New work was undertaken at Quercy by the group RCP 311 (Recherche cooperative sur programme 311) of the CNRS (Centre national de la Recherche scientifique), composed of researchers from the universities of Montpellier, Paris VI, and Lyon I. In the course of this recent work, the beds were excavated separately and each was well dated by means of its mammalian fauna (Crochet et al. 1972; de Bonis et al. 1973; Hartenberger 1973; Cavaillé et al. 1974; Hartenberger et al. 1974; Sigé 1974, 1976; Vianey-Liaud 1976; Sudre 1977; Crochet 1978).

I had undertaken the revision of the avifaunas of Quercy, and for that reason I was able to collect together the older documents kept in the collections of the National Museum of Natural History in Paris, the Natural History Museum and the Department of Earth Sciences of Lyon, and the University of Utrecht, as well as the newer documents amassed by the researchers of the University of Montpellier and the University of Paris VI.

The living trogons belong to a single family, the Trogonidae, a group of eight genera. Five of these live in Central America, South America, and the Antilles; two in tropical Africa, and one in southeast Asia (Peters 1945); see Figure 1. Trogons appear to have been a constant element of the paleoavifauna of Europe, ever since they were first described by Milne-Edwards (1867–1871) from the lower Miocene (Aquitanian) deposits of the department of Allier under the name of *Trogon gallicus*. (The generic name of this fossil form was later changed to *Paratrogon* by Lambrecht (1933).) Milne-Edwards (1892) subsequently discovered the presence of trogons in the Phosphorites du Quercy and created for these forms the genus *Archaeotrogon*. The new excavations at Quercy have shown that the trogons are often the most abundant elements in the avifauna, particularly in those beds that date from the upper Oligocene, such as Pech Desse, and above all, Pech du Fraysse. Futhermore, Olson (1976) has shown that one of the

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birds found in the "Glarner Fischschiefer" in Switzerland (see Fig. 1), and known as *Protornis glaronensis* von Meyer 1884, possessed the heterodactyl foot structure characteristic of the living trogons. Therefore, that specimen should be considered to be a member of the Trogonidae, even though the holotype of the species should be placed among the Momotidae; Peyer (1957) believed this species to be a member of the Alcedinidae. The age of the "Glarner Fischschiefer" is believed to be lower Oligocene (Sannoisian) because of the fish fossils found there. In addition to extinct forms of the European Tertiary, two living species of trogonids have been found as fossils in Pleistocene deposits: *Trogon surrucura* Vieillot in Brazil and *Temnotrogon roseigaster* (Vieillot) in the Dominican Republic (Brodkorb 1971).

SYSTEMATICS

Order Alcediniformes Feduccia 1977

Superfamily Trogonoidea Feduccia 1977

Archaeotrogonidae new family

TYPE GENUS: *Archaeotrogon* Milne-Edwards 1892

DIAGNOSIS: Trogons, that differ from all species of the family Trogonidae by lacking the heterodactyl foot characteristic of that family.

TEMPORAL AND GEOGRAPHIC DISTRIBUTION: Upper Eocene to lower Oligocene. Phosphorites du Quercy, France.

REMARKS: The family Archaeotrogonidae contains only the type genus. Although the archaeotrogons were characterized by the primitive structure of their tarsometatarsus, i.e., the lack of heterodactyly, in deposits of the same age as those at Quercy there existed a trogon whose foot already had a heterodactyl structure. One may therefore consider the forms of Quercy as a line parallel to that of the true trogons, which belong to the family Trogonidae. The Trogonidae contains the fossil bird from the Glarner Fischschiefer (Olson 1976), the extinct genus *Paratrogon,* as well as the living genera (*Pharomachrus, Euptilotis, Priotelus, Temnotrogon, Trogon, Apaloderma, Heterotrogon,* and *Harpactes*).

Genus *Archaeotrogon* Milne-Edwards 1892

TYPE SPECIES: *Archaeotrogon venustus* Milne-Edwards 1892

DESCRIPTION: *Archaeotrogon* has been described primarily on the basis of its humerus, and humeri are very abundant in the older collections. In addition to the humeri, Lydekker (1891) referred some coracoids (not figured) and Milne-Edwards (1892) some carpometacarpi (not figured) to the genus. Gaillard (1908) described and figured a tarsometatarsus that he attributed to the species *A. cayluxensis*. In certain sites at Quercy, specimens of *Archaeotrogon* are very numerous and represent more than half of the bird bones found in these beds. It is logical to assume that, if the most common humerus belongs to the genus *Archaeotrogon,* then the most common ulna, the most common carpometacarpus, the most common coracoid, etc., should likewise belong to that genus. I have therefore attributed to that genus a certain number of skeletal elements collected from all the sites where the humerus of *Archaeotrogon* was found, but it is also true that these elements show analogies with the corresponding bones of living trogons. I must point out that I have never found articulated bones in the Phosphorites du Quercy. This is probably due in part to the way the fossiliferous cavities were filled, and is partly a result of the methods of excavation, which included washing and screening techniques. There cannot, therefore, be an absolute certainty that the bones attributed to *Archaeotrogon* truly belong to that genus, but there is a strong probability that they do.

COMPARISON WITH LIVING TROGONIDAE. At the Natural History Museum of Leiden I was able to study skeletons belonging to the genera *Harpactes, Trogon, Pharomachrus,* and *Prioteles*. The genus *Archaeotrogon,* when compared with the Trogonidae, shows the following similarities and differences (characters of the Trogonidae in parentheses).

Humerus. Similarities: (1) same general form; (2) head enlarged and flattened; (3) internal trochanter very prominent; (4) tricipital fossa large; (5) pectoral crest lengthened; (6) distal extremity transversely widened; (7) tricipital grooves forming a large depression.

Differences: (1) proximal end very wide transversely (proximal end less wide transversely); (2) head rather flattened (head more swollen); (3) internal trochanter more strongly bent backwards and downwards; (4) no pneumatic orifice in the sub-trochanteric fossa (pneumatic orifices in the sub-trochanteric fossa); (5) tricipital fossa larger; (6) ligamental groove very long (ligamental groove rather short); (7) section of shaft flattened (corresponding section of shaft more circular); (8) impression of M. brachialis anticus long and shallow (impression of M. brachialis anticus more circular and sharply marked); (9) radial condyle rather long and narrow in the center (radial condyle much more rounded); (10) epitrochlea and epitrochlear prominence little developed (epitrochlea and epitrochlear prominence more developed and prominent on the internal side); (11) tricipital grooves very large and deep (tricipital grooves wide but not very deep); (12) external tricipital groove sharply marked and bordered by two raised crests (external tricipital groove less marked); (13) epicondyle well developed (epicondyle not very developed).

Ulna. Similarities: (1) general shape very similar; (2) same positioning of internal and external glenoid facets; (3) prominence for anterior articular ligament well marked; (4) shaft circular; (5) same general shape of distal end.

Differences: (1) proportionately shorter and more curved (longer and less curved); (2) glenoid surfaces oriented obliquely to long axis of bone (glenoid surfaces oriented almost parallel to long axis of bone).

Radius. Differences: (1) general form rectilinear (general form curved at distal end); (2) distal end spatulate, practically symmetrical to long axis of bone (distal end assymmetric).

Carpometacarpus. Similarity: Short and wide in both groups.

Differences: (1) radial apophysis forms a spur comparable to that seen in *Hoplopterus spinosus,* the Spurwing Plover; this radial apophysis was noted by Milne-Edwards (1892) (no spur in the genera *Harpactes, Trogon, Pharomachrus,* and *Prioteles*); (2) metacarpal III lies almost parallel to metacarpal II (metacarpal II at a very oblique angle to metacarpal III; the gap between the metacarpals is very wide at the distal end, and the distal end is very wide); (3) internal digital facet lies in the same plane as the external digital facet (internal digital facet lies at a different level than external digital facet).

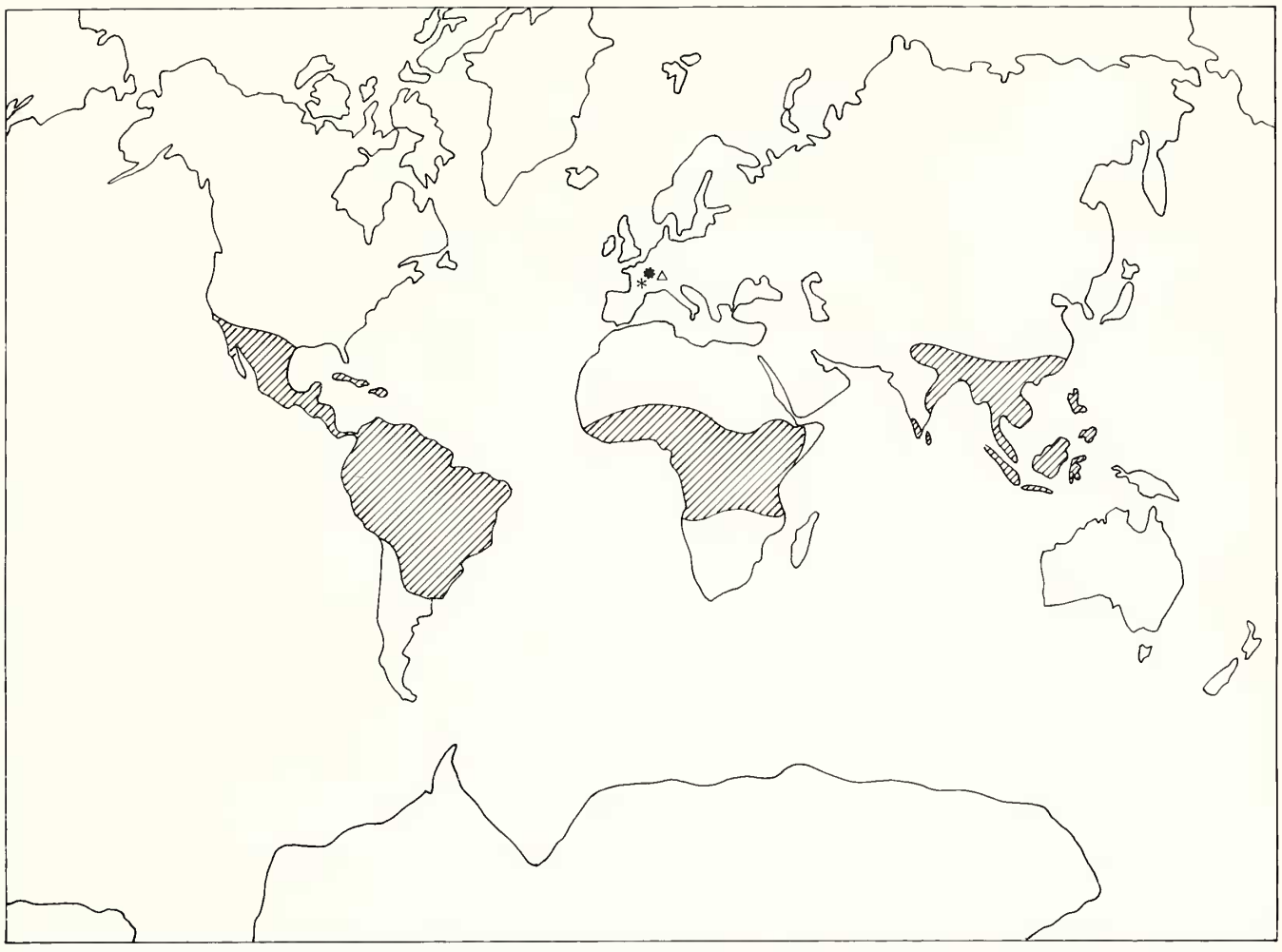

Figure 1. Geographic distribution of living trogons (hatching) and fossil trogons: (*) *Archaeotrogon,* Eocene and Oligocene, Phosphorites du Quercy, France; (✱) *Paratrogon,* Miocene of l'Allier, France; △ Trogonidae, Oligocene, Glarner Fischschiefer, Switzerland.

Coracoid. Similarities: (1) same general shape of the head, glenoid facet, and scapular facet; (2) no sub-clavicular foramen; (3) distal end large and paddle-shaped; (4) sternal facet almost perpendicular to the long axis of the bone.

Differences: (1) proportionately slightly shorter and more massive (proportionately longer and more slender); (2) sub-clavicular apophysis usually broken at the extremity, but rather wide at its origin (sub-clavicular apophysis narrow); (3) sternal facet short and strongly curved (sternal facet longer and not very curved); (4) hyosternal apophysis weakly developed on the external side and barely present on the internal side (hyosternal apophysis very well developed both externally and internally); (5) strongly marked groove for the ligament of the sterno-coracoidal muscle on the upper surface of the bone (very shallow groove for the sterno-coracoidal muscle).

Femur. Similarity: General shape very similar.

Differences: (1) proximal end rather flattened (proximal end more swollen); (2) no pneumatic orifice under the trochanter (pneumatic orifice present in the genus *Trogon,* but not in *Harpactes*); (3) fossa present below the articulation on the posterior side (no fossa present below the articulation on the posterior side); (4) shaft slender (shaft heavy in the genus *Trogon*, but slender in *Harpactes*); (5) distal end flattened (distal end more swollen).

Tibiotarsus. Similarities: (1) relatively short in both groups; (2) proximal articulation perpendicular to the long axis of the bone; (3) tibial crests poorly developed; (4) supratendinal bridge lies on the internal side of the bone; (5) shallow groove for the extensor muscle of the digits.

Differences: (1) shaft relatively slender and slightly widened toward the distal end (shaft heavier and widens toward the distal end); (2) external rugosity of oblique ligament well developed (external rugosity of oblique ligament poorly developed).

Tarsometatarsus. Similarity: Same general proportions as compared to the femur and tibiotarsus.

Differences: (1) internal trochlea turned slightly backward; digit I points backwards, digits II, III, and IV forwards (internal trochlea turned completely toward the rear; digits I and II point backwards, digits III and IV forwards); (2) hypotarsus with a channel pointing externally between two subequal calcaneal ridges (hypotarsus with a very strong median ridge (ridge 1) and two canals situated externally to that median ridge (see Fig. 2); (3) two very evident superior foramina, the

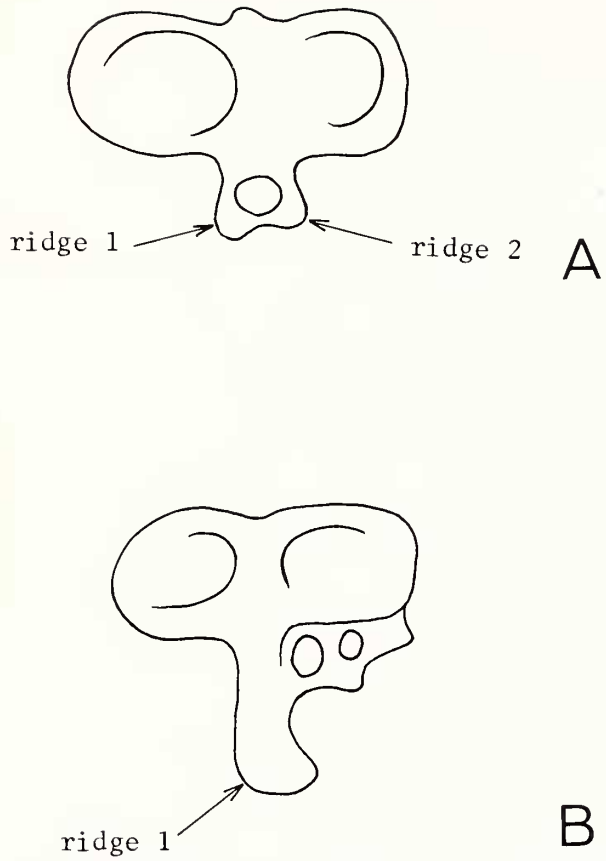

Figure 2. Diagram showing the position of the calcaneal ridges of the hypotarsus in the genus *Archaeotrogon* (A) and in the living genus *Trogon* (B). Right tarsometatarsus, proximal views.

internal foramen larger than the external foramen (two hardly noticeable superior foramina of equal size); (4) inferior foramen wide and in a deep groove, foramen lies clearly proximal to the trochleae (inferior foramen very small and in a shallow groove; foramen very close to trochleae); (5) shaft flattened anteroposteriorly (shaft rather flattened mediolaterally); (6) internal cotyla prominent and sharply defined (internal cotyla weak); (7) metatarsal facet well marked (metatarsal facet poorly marked).

It is the tarsometatarsus that shows the greatest contrast between the Archaeotrogonidae and the Trogonidae. *Archaeotrogon* does not have the heterodactyl foot characteristic of the living trogons and unique among all the birds.

Comparison with the Genus *Paratrogon* Lambrecht 1933. This genus contains the single species *Paratrogon gallicus* Milne-Edwards 1871, described from the Aquitanian deposits of Allier, and is known only from two humeri (Milne-Edwards 1867–1871:395–396, pl. 177, figs. 18–22).

The genus *Archaeotrogon* is noticeably different from *Paratrogon,* and contrary to the opinion of Lambrecht (1933), I believe that *Paratrogon* is closer to the living trogons than to *Archaeotrogon* and should therefore be placed in the family Trogonidae. When comparing the humerus of *Archaeotrogon* to that of *Paratrogon* one finds almost the same differences as noted between the humeri of *Archaeotrogon* and the living Trogonidae. The characters of the humerus are shown in Table 1.

Comparison with the Coraciiformes and the Caprimulgiformes. Feduccia (1977) has shown that the shape of the stapes, the middle ear ossicle in birds, can be used to show phylogenetic relationships. The trogonid stapes has a bulbous and hollow basal part with a large orifice on the posterior side, and a stapedial process arising from the edge of the basal part. This morphology is very different from the primitive morphology of the stapes, which is that of a flat discoidal plate with the stapedial process arising from its center. The trogon morphology of the stapes is found in four avian families previously assigned to the order Coraciiformes: Meropidae (bee-eaters), Alcedinidae (kingfishers), Momotidae (motmots), and Todidae (todys). According to Feduccia (1977:21), this similarity "argues strongly for monophyly of the trogons and bee-eaters/kingfisher/motmot/tody assemblage." The earlier classification has therefore been modified, and the four families mentioned above have been removed from the Coraciiformes and joined with the Trogonidae in the new order Alcediniformes. It would be interesting to know if the osteology of the primitive trogonids can support this relationship.

I was unable to compare *Archaeotrogon* with the Momotidae or the Todidae, which are restricted to the tropical zones of Central America and the Antilles, but I did make the comparison with the Meropidae and the Alcedinidae. There are similarities in the bones of the hindlimb of the latter two families and those of *Archaeotrogon,* but there are very great differences in the shape of the humerus.

In *Merops,* the proximal end of the humerus is not transversely widened, there is no tricipital fossa, the internal trochanter is low, the pectoral crest is short, the distal end is not very wide transversely and sits obliquely to the long axis of the shaft, the epitrochlea is very prominent toward the base, and the tricipital grooves do not occupy a deep and wide depression.

In the genera *Alcedo* and *Dacelo,* the head of the humerus is globular, the internal trochanter weakly developed, the subtrochanteric fossa very small, the pectoral crest very short, and the distal end is very different from that of *Archaeotrogon.*

On the other hand, there is a certain similarity between the humeri of *Archaeotrogon* and the living Caprimulgiformes (*Caprimulgus* and *Chordeiles*). This resemblance is particularly strong in the new species of *Archaeotrogon,* which has a crest obliquely crossing the tricipital fossa (see Figs. 4t–w, 10) as in the genus *Caprimulgus.* There are likewise other characters in common in both the humerus and other bones of the skeleton. The ancestral forms of the Caprimulgiformes are unknown, since the Aegialornithidae of the Eocene and Oligocene that have previously been placed in this order (Brodkorb 1971; Collins 1976) should actually belong to the Apodiformes (Harrison 1975; Mourer-Chauviré 1978). One may therefore speculate as to the possibility of *Archaeotrogon* being related to the Caprimulgiformes.

Archaeotrogon venustus Milne-Edwards 1892

Figure 3

1891 Genus b Lydekker, p. 78, fig. 3
1892 *Archaeotrogon venustus* Milne-Edwards, p. 5–7
1908 *Archaeotrogon venustus* Milne-Edwards, Gaillard, p. 66–67, fig. 14, pl. 3, figs. 20–23

Table 1. Morphological characters of the humerus of *Archaeotrogon, Paratrogon,* and the living Trogonidae.

Characters of the Humerus	*Archaeotrogon*	*Paratrogon*	Living Trogons
Proximal end	Very large and very recurved medially	Not large, slightly recurved medially	Not large, slightly recurved medially
Tricipital fossa	Large and usually shallow	Narrower	Narrower
Bicipital surface	Very wide transversely	Less wide transversely	Less wide transversely
Ligamental groove	Very long	Not very long	Not very long
Head of humerus	Rather flattened	More swollen	More swollen
Sub-trochanteric fossa	Without pneumatic orifices	Apparently without pneumatic orifices	Pneumatic orifices present
Impression of M. brachialis anticus	Long and shallow	More circular and deep	More circular and deep
Radial condyle	Lengthened and narrowed in the center	More globular	More globular
Epitrochlea	Poorly developed	Strongly developed	Strongly developed
Olecranal fossa	Very deep	Apparently rather deep	Rather shallow
Tricipital groove	Well marked externally and bordered by two prominent ridges	Weakly marked externally	Weakly marked externally and bordered by a ridge

1933 *Archaeotrogon venustus* Milne-Edwards, Lambrecht, p. 625

1971 *Archaeotrogon venustus* Milne-Edwards, Brodkorb, p. 247

1971 *Archaeotrogon venustus* Milne-Edwards, Crochet, p. 316

MATERIAL: Early collections without provenance: complete left humeri, QU 15797, QU 15799, QU 15805; incomplete left humeri, QU 15802, QU 15785; complete right humeri, QU 15781, QU 15782; incomplete right humerus, QU 15804; incomplete left carpometacarpi, QU 15917, QU 15939; complete right carpometacarpus, QU 15882; incomplete right carpometacarpi, QU 15915, QU 15918, QU 15940 (Museum of Paris). Incomplete right humerus, PQ 987; incomplete left humerus, PQ 991 (Museum of Lyon). Two left humeri and one right humerus almost complete (Department of Earth Sciences, Lyon).

Deposits of Pech du Fraysse: left humeri more or less complete, PFR 577, 578, 11034, 11147, 11186; proximal left humeri, PFR 11018, 11031, 11142, 11164, 11112, 11196; distal left humeri, PFR 580, 5105, 5109, 11040, 11188, 11187, 11055, 11056, 11123, 11155, 11062, 11160, 11201, 11116, 11117, 11229, 11230, 11231; shafts of left humeri, PFR 11042, 11191, 11093; right humeri more or less complete, PFR 5106, 5108, 11022, 11195; proximal right humeri, PFR 581, 9545, 11070, 11071, 11080, 11081, 11102, 11121, 11180, 11232, 11233, 11234; distal right humeri, PFR 579, 582, 583, 5107, 7218, 9802, 11029, 11033, 11045, 11046, 11051, 11061, 11066, 11080, 11108, 11149, 11150, 11157, 11189, 11190, 11191, 11192, 11194, 11197; shaft of right humerus, PFR 11063; left coracoids more or less complete, PFR 5112, 5113, 8583, 11058, 11083, 11084, 11085, 11100, 11109, 11124, 11161, 11235; proximal left coracoids, PFR 585, 7050, 11129, 11236; distal left coracoids, PFR 11237, 11238; right coracoids more or less complete, PFR 5111, 11076, 11088, 11095, 11133, 11162, 11166, 11168, 11172, 11205; proximal right coracoids, PFR 584, 8359, 11239; distal right coracoids, PFR 7465, 11126, 11174, 11251, 11240, 11241; left ulnae more or less complete, PFR 3998, 11047; proximal left ulnae, PFR 11098, 11111, 11125, 11204; distal left ulnae, PFR 5118, 9409, 11075, 11130, 11200, 11213; right ulnae more or less complete, PFR 11043, 11136, 11151; proximal right ulnae, PFR 8358, 11110, 11114, 11169, 11198, 11212; distal right ulnae, PFR 593, 594, 3999, 8360, 11068, 11170, 11208, 11242; left carpometacarpi more or less complete, PFR 576, 5110, 11073, 11074, 11167, 11216; proximal left carpometacarpi, PFR 7560, 11243, 11244, 11245, 11246, 11247; distal left carpometacarpi, PFR 586, 587, 7222, 11248, 11249; right carpometacarpi more or less complete, PFR 574, 575, 9546, 11086, 11089, 11090, 11115; proximal right carpometacarpi, PFR 11099, 11127, 11128, 11202, 11250, 11251, 11252; distal right carpometacarpi, PFR 11105, 11253; proximal scapulae, PFR 11103, 11254, 11255, 11256, 11257; distal radii, PFR 11258, 11259, 11260, 11261, 11262, 11263; left femora more or less complete, PFR 11082, 11105; proximal left femur, PFR 11107; distal left femur, PFR 11264; right femora more or less complete, PFR 11060, 11113; proximal right femur, PFR 11265; distal right femora, PFR 11211, 11214, 11266; proximal left tibiotarsus, PFR 11131; distal left tibiotarsus, PFR 11267; almost complete right tibiotarsus, PFR 11203; distal right tibiotarsi, PFR 11096, 11132, 11268; almost complete left tarsometatarsi, PFR 11091, 11175, 11269; distal left tarsometatarsi, PFR 11270, 11271, 11272, 11273; distal right tarsometatarsi, PFR 11274, 11275, 11276, 11277 (Museum of Paris).

Deposits of Escamps A: proximal scapula.

Deposits of Itardies: distal left humerus ITD 548; distal right humeri, ITD 569, 617; proximal right coracoids, ITD 542, 573, 704, 709; distal right coracoid, ITD 691; proximal left ulnae, ITD 678, 684; proximal right ulna, ITD 538; distal right

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ulna, ITD 673; proximal left carpometacarpi, ITD 696, 710; distal left carpometacarpus, ITD 541; proximal right carpometacarpus, ITD 575.

Deposits of Mas de Got B: complete right carpometacarpus, MGB 1545; distal right femur, MGB 1558.

Deposits of Mounayne: proximal right carpometacarpus, MOU 1.

Deposits of Pech Desse: complete left humeri, PDS 1226, 1236; distal left humeri, PDS 1218, 1227, 1234; almost complete right humerus, PDS 1212; proximal right humerus, PDS 1257; distal right humeri, PDS 1223, 1232, 1274; almost complete left coracoids, PDS 1230, 1237; proximal left coracoid, PDS 1243; complete right coracoid, PDS 1244; proximal right coracoid, PDS 1275; distal right coracoid, PDS 1242; proximal left ulna, PDS 1235; distal left ulnae, PDS 1249, 1252, 1269, 1270; distal right ulnae, PDS 1241, 1260; distal right carpometacarpus, PDS 1264; proximal scapulae, PDS 1271, 1278, 1281, 1289; almost complete left femur, PDS 1277; distal right femur, PDS 1280; distal left tarsometatarsus, PDS 1273.

Deposits of Perrière: distal left ulnae, PRR 2599, 2609; proximal left carpometacarpus, PRR 2608; proximal left femur, PRR 2607.

Deposits of La Plante 2: distal left humerus, PLA 1047; shaft of right humerus, PLA 1062; proximal right coracoid, PLA 1071; distal right coracoid, PLA 1066; proximal right ulna, PLA 1065; distal right ulna, PLA 1063; complete right carpometacarpus, PLA 1064; proximal left carpometacarpus, PLA 1073; proximal right carpometacarpus, PLA 1070; proximal scapula, PLA 1069; wing phalanx?, PLA 1067.

Deposits of Roqueprune 2: complete left coracoid, ROQ 310; distal right coracoid ROQ 317; proximal left ulna, ROQ 315; distal right ulna, ROQ 312; distal left femur, ROQ 313; proximal right femur, ROQ 311; proximal scapula, ROQ 318 (University of Montpellier and Paris VI).

Deposits of Boussac 1: almost complete left carpometacarpus.

Deposits of Boussac 2: distal right ulna and distal left ulna.

Deposits of Escamps 3: distal right humerus.

Deposits of Fonbonne 1: proximal left coracoid.

Deposits of Garrigues: proximal right carpometacarpus (University of Utrecht).

DESCRIPTION: *Archaeotrogon venustus* is the smallest species in the genus. It is also the species most abundantly represented in the recently collected material and the best known in regards to the skeleton. All the characters previously indicated in the description of the genus *Archaeotrogon* apply to this species.

MEASUREMENTS: For measurements of this species see Table 2.

Archaeotrogon zitteli Gaillard 1908

Figure 4a–j

1908 *Archaeotrogon zitteli* Gaillard, p. 69, fig. 16; p. 70–72, fig. 17, pl. 3, figs. 24–25 and 26–27

1933 *Archaeotrogon zitteli* Gaillard, Lambrecht, p. 626

1971 *Archaeotrogon zitteli* Gaillard, Brodkorb, p. 246–247

MATERIAL: Early collections without provenance: almost complete left humeri, QU 15787, 15790, 15791, 15792a, 15792b, 15795; proximal left humerus, QU 15788; distal left humeri, QU 15784, 15793, 15947; almost complete right humeri, QU 15783, 15789, 15798, 15801; almost complete left coracoid, QU 15911; almost complete left carpometacarpi, QU 15647, 15927; almost complete right carpometacarpi, QU 15659, 15662, 15928, 15934, 15942, 15944; proximal right carpometacarpus, QU 15946 (Museum of Paris). Complete left humerus, PQ 1053, cast of no. 128 from the Museum of Munich, holotype; complete right humerus, PQ 1052, cast from the Museum of Munich (referred to *A. venustus* by Gaillard (1908), but its size actually corresponds to *A. zitteli*); distal right humerus, PQ 990; 3 left and 2 right tarsometatarsi, 4 of which are almost complete, PQ 1069 (One of these was figured by Gaillard (1908, fig. 16 and pl. 3, fig. 26–27) and attributed to *A. cayluxensis,* but it has suffered a little damage since then.) (Museum of Lyon).

Deposits of Pech du Fraysse: complete left carpometacarpi, PFR 11069, 11097; distal left ulna, PFR 11092 (Museum of Paris).

Deposits of Mas de Got B: complete left ulna, MGB 1548; complete right ulna, MGB 1555; almost complete left coracoid, MGB 1553 (University of Montpellier).

Deposits of Belgarite IVa: incomplete right humerus (University of Utrecht).

DESCRIPTION: According to Gaillard (1908:70), the humerus of *Archaeotrogon zitteli* is quite well distinguished anatomically from that of *A. venustus*. He stated that in *A. zitteli* the head of the humerus is much more widened transversely, the tricipital fossa is shallower, and on the anterior face, the bicipital surface is much reduced. I was able to study a large number of humeri of both species, and these morphological differences seem to me to be attributable to individual variation. The head of the humerus does not appear to be wider transversely, nor the bicipital surface smaller in *A. zitteli*. The tricipital fossa is perhaps slightly shallower in *A. zitteli,* but this character is rather variable. Certain specimens such as QU 15798 (Fig. 4d) have a shallow tricipital fossa, while others such as QU 15795 (Fig. 4c) have a much deeper tricipital fossa.

It appears to me that the principal character that distinguishes *A. zitteli* from *A. venustus* is size, the former species

←

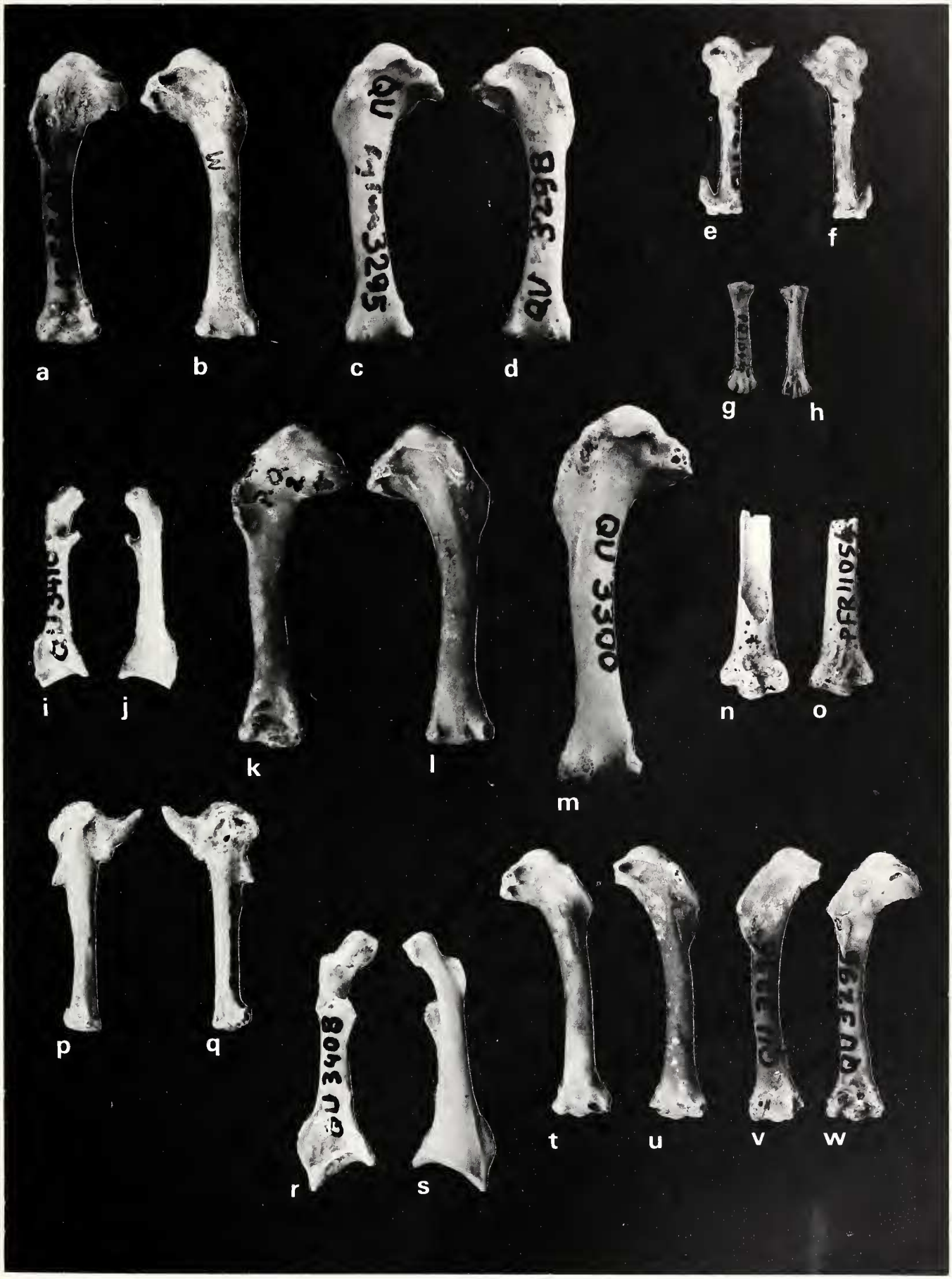
Figure 3. Specimens of *Archaeotrogon venustus*. Complete right humerus, QU 15782 (formerly QU 3282), Museum of Paris, ×3.9, in anconal (a) and palmar (b) view. Complete right coracoid, PFR 11168, Museum of Paris, ×3.6, in anterior (c) and posterior (d) view. Complete right ulna, PFR 11047, Museum of Paris, ×3.7, in external (e) and internal (f) view. Complete right carpometacarpus, MGB 1545, University of Montpellier, ×3.7, in internal (g) and external (h) view. Proximal right scapula, PFR 11254, Museum of Paris, ×3.6, in dorsal (i) view. Distal radius, PFR 11258, Museum of Paris, ×3.7, in external (j) and internal (k) view. Complete left femur, PFR 11082, Museum of Paris, ×3.7, in posterior (l) and anterior (m) view. Complete left tarsometatarsus, PFR 11091, Museum of Paris, ×3.7, in anterior (o) and posterior (p) view. Distal right tibiotarsus, PFR 11132, Museum of Paris, ×3.7, in anterior (q) view. Incomplete right tibiotarsus, PFR 11203, Museum of Paris, ×3.7, in posterior (r) view.

Table 2. Measurements (mm) of *A. venustus* and *A. zitteli* bones.

	Archaeotrogon venustus					*Archaeotrogon zitteli*				
	n	min.	max.	mean	variance s2	n	min.	max.	mean	variance s2
Humerus										
Length	20	25.0	29.7	27.82	1.31	12	30.1	33.4	31.43	0.84
Width head	27	8.4	9.4	8.85	0.07	9	9.4	10.3	9.98	0.06
Width distal end	56	5.8	7.2	6.30	0.11	16	6.8	7.5	7.13	0.03
Width shaft in the middle	92	2.6	3.3	2.91	0.02	18	3.2	3.7	3.48	0.03
Ulna										
Length	4	28.0	29.5	28.80	0.66	2	30.7	30.9	30.80	0.02
Width head	21	4.0	4.7	4.30	0.03	2	4.5	4.9	4.70	0.08
Width distal end	30	3.4	4.0	3.73	0.02	3	4.0	4.4	4.17	0.04
Depth distal end	30	3.6	4.2	3.84	0.03	3	4.1	4.3	4.20	0.01
Width shaft in the middle	39	2.0	2.4	2.17	0.01	3	2.3	2.4	2.33	0.003
Radius										
Width distal end	6	3.0	3.5	3.18	0.03					
Width shaft in the middle	6	1.1	1.2	1.17	0.003					
Carpometacarpus										
Length	21	17.8	19.8	18.84	0.18	10	19.5	20.9	20.27	0.36
Width head	32	6.2	7.8	7.08	0.20	10	7.5	8.3	7.85	0.08
Width distal end	25	3.6	4.5	4.01	0.07	7	4.0	4.8	4.46	0.08
Width metacarpal 2 in the middle	42	1.5	2.0	1.85	0.02	10	1.9	2.1	1.98	0.006
Coracoid										
Length	23	18.8	21.7	20.50	0.42	2	22.7	24.0	23.35	0.85
Width head	38	3.8	4.9	4.30	0.07	2	4.3	4.5	4.40	0.02
Width sternal end	19	4.7	6.2	5.34	0.16	2	6.2	6.2	6.20	0.00
Width shaft in the middle	46	1.9	2.7	2.22	0.03	3	2.3	2.6	2.43	0.02
Femur										
Length	5	22.0	22.4	22.34	0.16					
Width head	7	4.4	4.8	4.59	0.03					
Width distal end	7	4.2	4.5	4.36	0.01					
Width shaft in the middle	13	1.7	2.0	1.83	0.01					
Tibiotarsus										
Length	1			~29						
Width head	2	3.4	3.9	3.65	0.13					
Width distal end	4	3.7	4.1	3.83	0.04					
Width shaft in the middle	4	1.6	1.7	1.65	0.003					
Tarsometatarsus										
Length	2	16.2	16.6	16.40	0.08	5	15.8	16.7	16.26	0.15
Width head	3	4.0	4.4	4.23	0.04	4	4.0	4.2	4.08	0.01
Width distal end	5	3.8	4.1	3.96	0.02	4	3.8	4.5	4.18	0.09
Width shaft in the middle	7	1.7	1.9	1.79	0.005	5	1.9	2.3	2.04	0.02

→

Figure 4. Specimens of *Archaeotrogon*. *A. zitteli*: Complete right humerus, QU 15801 (formerly QU 3301), Museum of Paris, ×1.7, in palmar (a) and anconal (b) view. Complete left humerus, QU 15795 (formerly QU 3295), Museum of Paris, ×1.9, in anconal (c) view. Complete right humerus, QU 15798 (formerly QU 3298), Museum of Paris, ×1.9, in anconal (d) view. Almost complete left carpometacarpus, QU 15927 (formerly QU 3427), Museum of Paris, ×1.8, in internal (e) and external (f) view. Almost complete left tarsometatarsus, PQ 1069, Museum of Lyon, ×1.3, in anterior (g) and posterior (h) view. Complete left coracoid, QU 15910 (formerly QU 3410), Museum of Paris, ×1.7, in posterior (i) and anterior (j) view. *A. cayluxensis*: Complete right humerus, holotype, PQ 2, Museum of Lyon, ×1.7, in palmar (k) and anconal (l) view. Complete left humerus, QU 15800 (formerly QU 3300), Museum of Paris, ×1.9, in anconal (m) view. Distal right ulna, PFR 11054, Museum of Paris, ×1.9, in internal (n) and external (o) view. Complete right carpometacarpus, QU 15949 (formerly QU 3449), Museum of Paris, ×1.7, in external (p) and internal (q) view. Complete left coracoid, QU 15908 (formerly QU 3408), Museum of Paris, ×1.7, in posterior (r) and anterior (s) view. *A. hoffstetteri* new species: Almost complete right humerus, holotype, QU 15796 (formerly QU 3296), Museum of Paris, ×1.7, in anconal (t) and palmar (w) view. Almost complete right humerus, paratype, QU 15786 (formerly QU 3286), Museum of Paris, ×1.7, in anconal (u) and palmar (v) view.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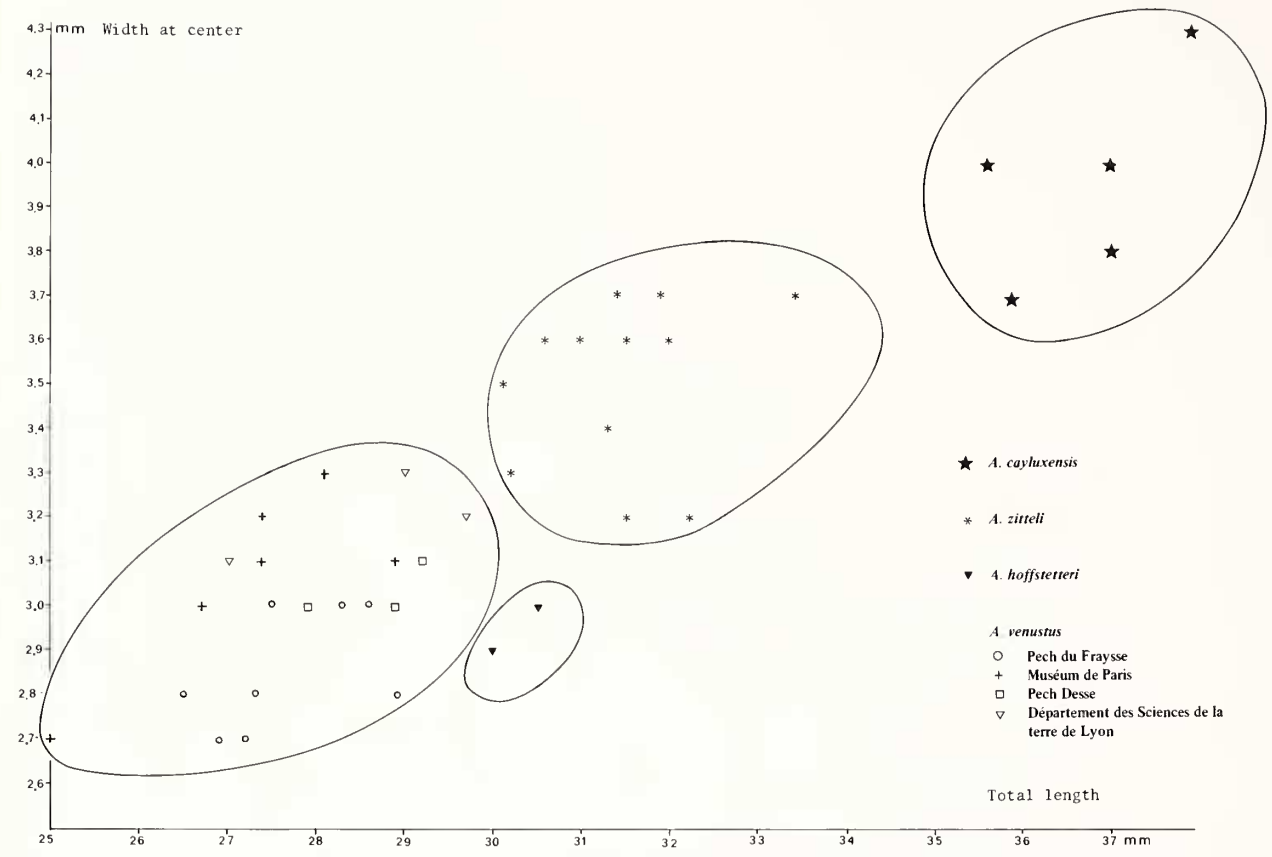

Figure 5. Scatter diagram for the humeri of the different species of *Archaeotrogon* from the Phosphorites du Quercy.

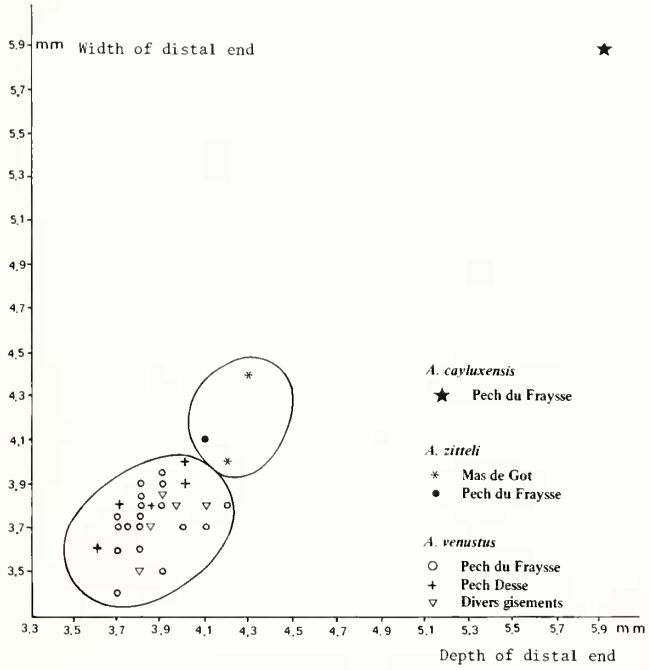

Figure 6. Scatter diagram for the distal end of the ulnae of *Archaeotrogon venustus*, *A. zitteli*, and *A. cayluxensis*.

being the larger. In the scatter diagrams (Figs. 5–9), they form distinct clusters of points. The measurements of the bones attributed to *A. zitteli* are shown in Table 2. They are slightly larger than those of *A. venustus*, and on the whole there is very little overlap in the measurements of the two species. This cannot be an example of evolution, i.e., the smaller *A. venustus* evolving into the larger *A. zitteli*, as both species have been discovered together in at least two sites in the new excavations at Quercy: Mas de Got B, of the lower Oligocene, and Pech du Fraysse, of the upper Oligocene.

I have referred to *A. zitteli* five tarsometatarsi from the Museum of Lyon (PQ 1069), one of which was figured by Gaillard (1908) and described as *A. cayluxensis*. The size of *A. cayluxensis* is much larger than that of either *A. venustus* or *A. zitteli*. Practically all the specimens of *Archaeotrogon* found at Pech du Fraysse belong to *A. venustus*, and it seems likely that the tarsometatarsi, especially the two complete ones (PFR 11091, 11175), likewise belong to this species. In the scatter diagram of the tarsometatarsus (Fig. 9), it is evident that the specimens numbered PQ 1069 have a total length comparable to that of the *A. venustus* from Pech du Fraysse, but their shafts are much thicker. It seems to me, therefore, that these tarsometatarsi belong to *A. zitteli*, all the more so since *A. zitteli* is far more numerous in the early collections than *A. venustus*. It is logical to assume that if one finds many humeri one should also have a few foot bones.

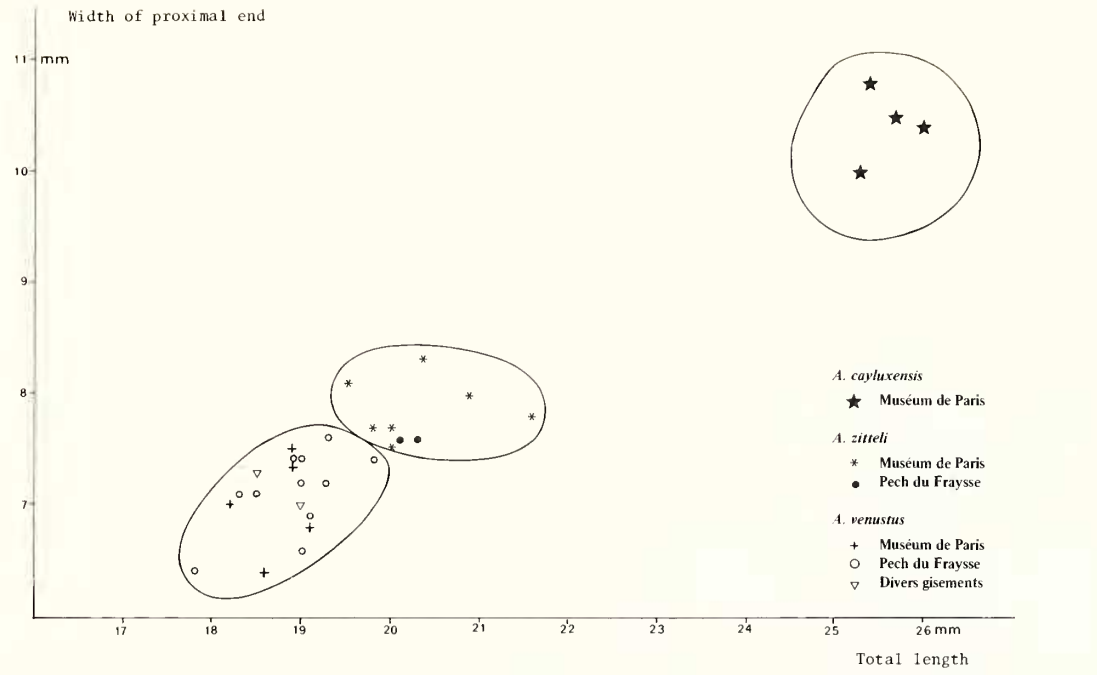

Figure 7. Scatter diagram for the carpometacarpi of *Archaeotrogon venustus, A. zitteli,* and *A. cayluxensis.*

Archaeotrogon cayluxensis Gaillard 1908

Figure 4k–s

1908 *Archaeotrogon cayluxensis* Gaillard, p. 67–70, fig. 15, pl. 4, figs. 1–4

1933 *Archaeotrogon cayluxensis* Gaillard, Lambrecht, p. 625–626

1939 *Archaeotrogon cayluxensis* Gaillard, Gaillard, p. 17–18, fig. 7

1971 *Archaeotrogon cayluxensis* Gaillard, Brodkorb, p. 246

MATERIAL: Early collections without provenance: almost complete left humeri, QU 15778, 15779, 15800; distal left humeri, QU 15780, 15803, 15806; distal right humerus, QU 15794; complete left coracoid, QU 15908; complete right coracoid, QU 15907; complete right carpometacarpi, QU 15916, 15924, 15948, 15949, 15950; proximal left carpometacarpi, QU 15668, 15944 (Museum of Paris). Complete right humerus, PQ 2 (Holotype of Gaillard); distal left humerus, cast without number (Museum of Lyon). Almost complete right humerus, figured in Gaillard (1939, fig. 7) (Department of Earth Sciences, Lyon).

Deposits of Pech du Fraysse: distal right ulna, PFR 11054 (Museum of Paris).

DESCRIPTION: Gaillard (1908:67) says that the humerus of *A. cayluxensis* differs from that of *A. venustus,* not only in size, but also in the following anatomical characters: in *A. cayluxensis,* the head of the humerus is thicker anteroposteriorly, the tricipital fossa and the sub-trochanteric fossa are large and shallow, the pectoral crest is long with a rounded edge, the bicipital surface is smaller in a vertical direction, the body of the humerus is more slender and widened toward the distal end, the epitrochlea and epicondyle are more prominent, and the inferior groove of the triceps is deeper.

Having been able to examine more material, certain of these distinctive characters seem valid and others less so. I would agree that the head of the humerus is thicker anteroposteriorly in *A. cayluxensis,* the bicipital surface is proportionately smaller, the epitrochlea and the epicondyle are more prominent, and the triceps groove is deeper. Further, the radial condyle is proportionately much more developed anteroposteriorly.

The form of the tricipital fossa is rather variable among individuals, being very shallow in the holotype, PQ 2 (Fig. 4l), but much deeper in other specimens, such as QU 15800 (Fig. 4m). The shape of the sub-trochanteric fossa appears no different than that of *A. venustus,* and the pectoral crest is not especially longer, nor is its border more rounded. The shaft is slender in the holotype, but it is much heavier in other individuals, for example, QU 15800 (Fig. 4m). It does not seem to widen more toward the base than does *A. venustus.* The most important distinguishing character is certainly the size, which is clearly superior to *A. venustus* and *A. zitteli* (Figs. 5–8).

Archaeotrogon cayluxensis is known mostly from the early collections. Only a single bone attributable to this species has been found in the recent collections from Quercy. It is a distal ulna from Pech du Fraysse (PFR 11054, Fig. 4n–o). Its morphology corresponds to that of the genus *Archaeotrogon,* and its size is very important (Fig. 6).

If one calculates the ratios of the means of the measurements of all the bones of the two species *A. cayluxensis* and *A. venustus,* the result varies from 1.28 to 1.52. If the same ratios are taken between *A. cayluxensis* and *A. zitteli,* the results vary from 1.14 to 1.43. This means that *A. cayluxensis* is an average of 1.28 to 1.52 times as large as *A. venustus,* and 1.14 to 1.43 times as large as *A. zitteli.* If one takes the only two measurements possible on the ulna from Pech du Fraysse and

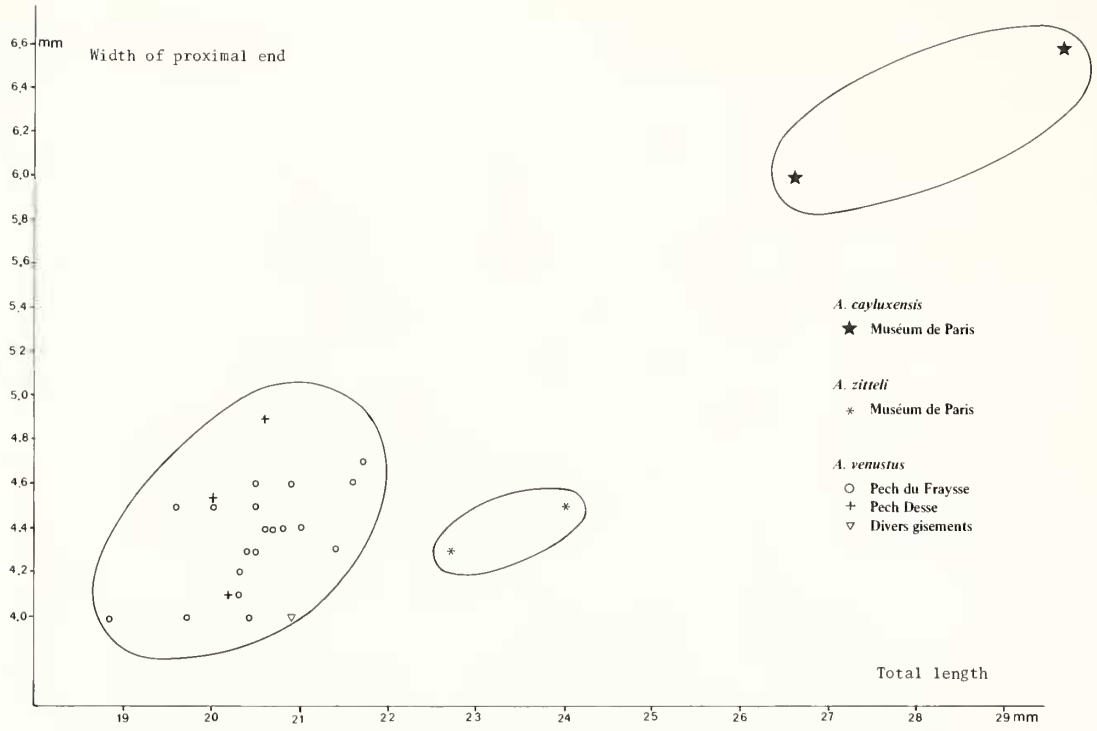

Figure 8. Scatter diagram for the coracoids of *Archaeotrogon venustus*, *A. zitteli*, and *A. cayluxensis*.

compares them with the mean values for the corresponding measurements of the other two species, the following ratios result: with *A. venustus*, 1.58 (depth) and 1.54 (width); with *A. zitteli*, 1.41 (depth) and 1.40 (width). The ratios between the measurements of the ulna from Pech du Fraysse and those of the other two species are therefore slightly larger than those generally observed between *A. cayluxensis* on the one hand, and *A. venustus* and *A. zitteli* on the other. But the ulna falls within the range of individual variation. It may belong to a particularly robust individual of *A. cayluxensis*.

MEASUREMENTS: For measurements of this species see Table 3.

Archaeotrogon hoffstetteri new species

Figure 4t–w

HOLOTYPE: Complete right humerus, QU 15796, National Museum of Paris.

PARATYPE: Slightly incomplete right humerus, QU 15786, National Museum of Paris.

TYPE LOCALITY: Phosphorites du Quercy, France.

TYPE STRATA: Upper Eocene or Oligocene.

DIAGNOSIS: A species of the genus *Archaeotrogon*, characterized by having a humerus of about the same size as that of *A. venustus* or *A. zitteli*, but with a much more slender

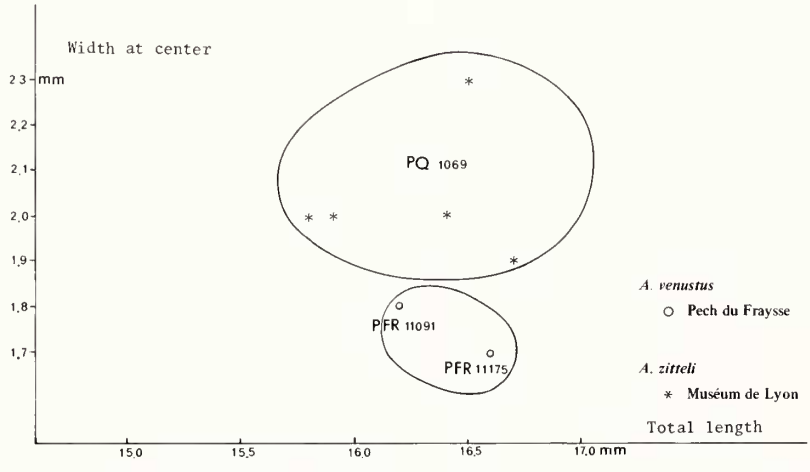

Figure 9. Scatter diagram for the tarsometatarsi of *Archaeotrogon venustus* and *A. zitteli*.

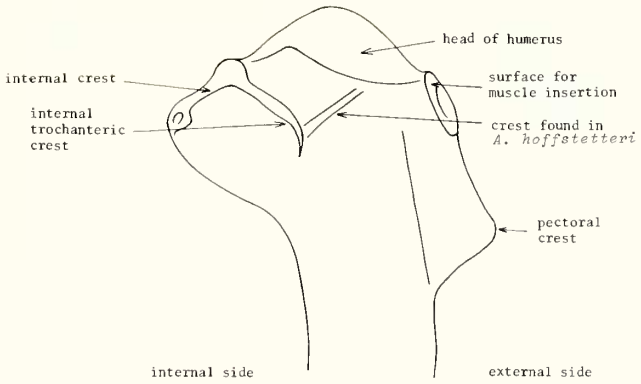

Figure 10. Diagram of the proximal end of the humerus of *Archaeotrogon hoffstetteri* new species, in anconal view.

shaft and with the proximal end much more recurved internally.

ETYMOLOGY: This species is named in honor of Dr. Robert Hoffstetter.

DESCRIPTION: These two humeri are sharply separated from the other humeri of *Archaeotrogon* by their slenderness and by the sigmoid curve of their shafts. Where the other humeri of *Archaeotrogon* are massive, these appear much more slender. Further, the proximal end of the bone is strongly twisted inwards.

On the posterior side of the bone, the tricipital fossa is very shallow. The sub-trochanteric fossa, under the internal trochanter, is bordered by two crests, an internal crest and a crest that Milne-Edwards called the internal trochanteric crest (Fig. 10). In *A. hoffstetteri,* another crest arises from the base of this internal trochanteric crest and leads toward the head of the humerus, crossing the tricipital fossa obliquely.

Below the external trochanter is a muscle insertion surface that is rather elongate and lies parallel to the long axis of the bone in *A. venustus, A. zitteli,* and *A. cayluxensis.* In *A. hoffstetteri* this surface is proportionately shorter and lies more obliquely.

In *A. hoffstetteri,* on the external face of the bone, the pectoral crest is very prominent and its upper edge shows a marked swelling. This pectoral crest is equally as prominent on the anterior side of the bone, and the bicipital surface is rather poorly developed.

The distal end of the bone does not show any particular characters, the more so since it is imperfectly preserved in both humeri attributed to this species.

RELATIONSHIPS AND DIFFERENCES: This species can be distinguished from *A. cayluxensis* by its much smaller size. The total length of the humerus is comparable to the largest among *A. venustus* or the smallest among *A. zitteli,* yet though the length is comparable, the shaft is far more slender in *A. hoffstetteri* (Fig. 5). Further, the bone has a characteristically sinuous shape. In addition, there are the other distinct morphological characters, i.e., a crest that obliquely crosses the tricipital fossa, the length and orientation of the muscle insertion scar below the external trochanter, and the very strong development of the pectoral crest in *A. hoffstetteri* (Fig. 10).

MATERIAL AND LOCALITIES: This species is represented only by the two humeri in the collections of the National Museum of Natural History in Paris, and is not represented in the newer collections from the Phosphorites du Quercy. The original locality is unknown, and it is impossible to assign it a precise geological age. It is possible that among the skeletal elements, other than the humeri, at present assigned to *A. venustus* and *A. zitteli,* certain bones may prove to belong to *A. hoffstetteri.* There is always the hope that this species may

Table 3. Measurements (mm) of *A. cayluxensis* and *A. hoffstetteri* bones.

	Archaeotrogon cayluxensis					*Archaeotrogon hoffstetteri*				
	n	min.	max.	mean	variance s2	n	min.	max.	mean	variance s2
Humerus										
Length	5	35.6	37.9	36.68	0.87	2	30.0	30.5	30.25	0.13
Width head	3	11.8	12.0	11.90	0.01	1			8.7	
Width distal end	10	7.5	8.5	8.18	0.12	2	6.3	6.8	6.55	0.13
Width shaft in the middle	10	3.7	4.3	4.05	0.04	2	2.9	3.0	2.95	0.005
Ulna										
Width distal end	1			5.9						
Depth distal end	1			5.9						
Carpometacarpus										
Length	5	24.7	25.7	25.42	0.24					
Width head	6	10.0	10.9	10.58	0.13					
Width distal end	4	4.9	5.4	5.13	0.05					
Width metacarpal II in the middle	6	2.4	2.6	2.53	0.01					
Coracoid										
Length	2	26.6	29.7	28.15	4.81					
Width head	2	6.0	6.6	6.30	0.18					
Width sternal end	2	7.4	8.8	8.10	0.98					
Width shaft in the middle	2	3.1	3.3	3.20	0.02					

Table 4. Temporal distribution of Trogoniformes in the deposits of the Phosphorites du Quercy. Mammal zones after Fahlbusch (1975).

	Stages and Absolute Age in my	Zones of Nannoplankton after Martini	Mammal Zones	Deposits of the Phosphorites du Quercy	Species of Trogoniformes
OLIGOCENE	Stampian 26	NP 24	Boningen	Pech du Fraysse	*A. venustus*, *A. zitteli*, *A. cayluxensis*
				Pech Desse	*A. venustus*
			Antoingt		
			Heimersheim		
		NP 23	Montalban	Itardies	*A. venustus*
				Mounayne	*A. venustus*
	32		Villebramar	Mas de Got B	*A. venustus*, *A. zitteli*
				La Plante 2	*A. venustus*
		NP 22		Roqueprune 2	*A. venustus*
			Hoogbutsel		
	"grande coupure"				
EOCENE	Priabonian 36	NP 21	Frohnstetten		
		NP 20	Montmartre—San Cugat	Escamps	*A. venustus*
	39		La Débruge		
		NP 19	Perrière	Perrière	*A. venustus*
		NP 18	Fons 4		
	41 Bartonien s. st.	NP 17	Grisolles		

reappear in the course of new research on the phosphorites, and that we may then learn more of its skeleton.

MEASUREMENTS: For measurements of this species see Table 3.

TEMPORAL DISTRIBUTION

The distribution of the different species of the genus *Archaeotrogon* in the sites of the Quercy phosphorites is shown in Table 4. It is evident that *A. venustus,* which is the species most numerous in the recent collections, has a very large temporal range. It is already present in the Perrière zone, and persists at least until the Boningen, stretching across a length of at least ten mammal zones. In absolute terms this time span can be evaluated at nearly 15 million years.

The species *A. zitteli* and *A. cayluxensis,* quite common in the early collections, have been rediscovered in the course of the recent excavations in only two sites (Mas du Got B and Pech du Fraysse). It is therefore not possible to precisely determine their temporal distribution.

The Archaeotrogonidae are relatively rare, but are nonetheless found in beds antedating the "grande coupure," or "great change," such as those of Perrière and Escamps. This great change is practically on the Eocene-Oligocene boundary and is characterized by a large-scale replacement among the mammalian fauna. In the upper Eocene beds at Quercy, the predominant forms among the birds belong to the Aegialornithidae. In contrast, after the great change, it is the Archaeotrogonidae that become predominant while the genus *Aegialornis* disappears. The Aegialornithidae still existed, but they are represented only by the genus *Cypselavus,* which is always rather rare. As for the mammals, the "grande coupure" seems to correspond to a rather important change in the avian world.

ACKNOWLEDGMENTS

I thank J.P. Lehman, Director of the Institute of Paleontology of the National Museum of Natural History of Paris; L. David, Director of the Natural History Museum of Lyons; and H. de Bruijn of the University of Utrecht for having kindly loaned me part of the material studied herein. I thank as well my colleagues from the University of Paris VI and the University of Montpellier for having kindly entrusted me with the study of the materials that they collected in their excavations. The Netherlands Organization for Scientific Research (ZWO) made it possible for me to visit the Rijksmuseum van Natuurlijke Historie of Leiden in order to compare the fossil birds from Quercy with living exotic forms. Finally, I thank K.A. Hünermann of Zurich for the precise data he gave me regarding the age of the "Glarner Fischschiefer."

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